

PALEOGENE PHYTOGEOGRAPHY AND CLIMATOLOGY OF SOUTH AMERICA¹

EDGARDO J. ROMERO²

ABSTRACT

Paleogene, Maastrichtian, and Miocene floras are reviewed. They are located on continental margins, where several sedimentary basins developed. The affinities of the fossil genera to living ones allow the recognition of three paleofloras: Neotropical, Mixed, and Antarctic. These could be the forerunners, respectively, of the presently more humid dominions in Neotropical Region (Caribbean, Amazonic, and Guayano), of the drier ones (Chaqueño and Andino-Patagonico), and of the Subantarctic Dominion of the Antarctic Region. The South American climate, as indicated by the fossil floras, showed a trend to higher temperatures during the Paleocene and Lower Eocene, and a deterioration through the Middle and Upper Eocene.

The purpose of the present work is to review the Paleogene taphofloras of South America and to analyze their paleophytogeographical and paleoclimatical significance.

This problem has interested botanists and paleontologists in the past. Berry (1921, 1938, 1940) published several reviews as a direct result of his work in the continent. More recently, Menéndez (1964, 1969, 1971) detailed the taphofloras and the areas occupied by the different types of vegetation, and Volkheimer (1971) gathered evidence about the paleoclimatology of Argentina. Later, Archangelsky and Romero (1974) analyzed the environmental conditions based on the pollen record of the southern South American Paleogene, and Aragón and Romero (1984), Romero (1978), Romero and Arguijo (1981b, 1982), and Romero and Dibbern (1984) analyzed some taphofloras of the same region. Therefore, much new geological, botanical, and paleontological evidence has been gathered, warranting a new review.

The present paper is arranged in two parts. The first one reviews every published outcrop with impressions known to the author from the Paleogene of South America, complemented with information about fruit casts, petrified wood, and palynology. Data about some Maastrichtian and Miocene floras have been added to show more general trends in the changes. The age of the deposits was updated according to recent publications. The second part discusses the phytogeographical areas that could have existed during that time, and the climate under which they have developed.

There is not an agreement on the terminology to be used in biogeographical discussions, especially among paleobotanists. I shall use a few of them, in an attempt to reach more accuracy and clarity, but without discussing their antecedents or convenience, which surpasses the limits of the present paper. They are:

Flora. The list of the plants living together in a given area at a given moment. They may be fossil or living.

Vegetation. Plant cover in a given area at a given moment, fossil or living. Their association, ecology, and life forms, rather than their taxonomic identity, are considered.

Taphoflora. The list of the fossil plants preserved in a given outcrop. They represent the original flora, as affected by dispersal, burial in that place, diagenesis, and differential alteration. They are the smallest real evidence to be used in paleophytogeography.

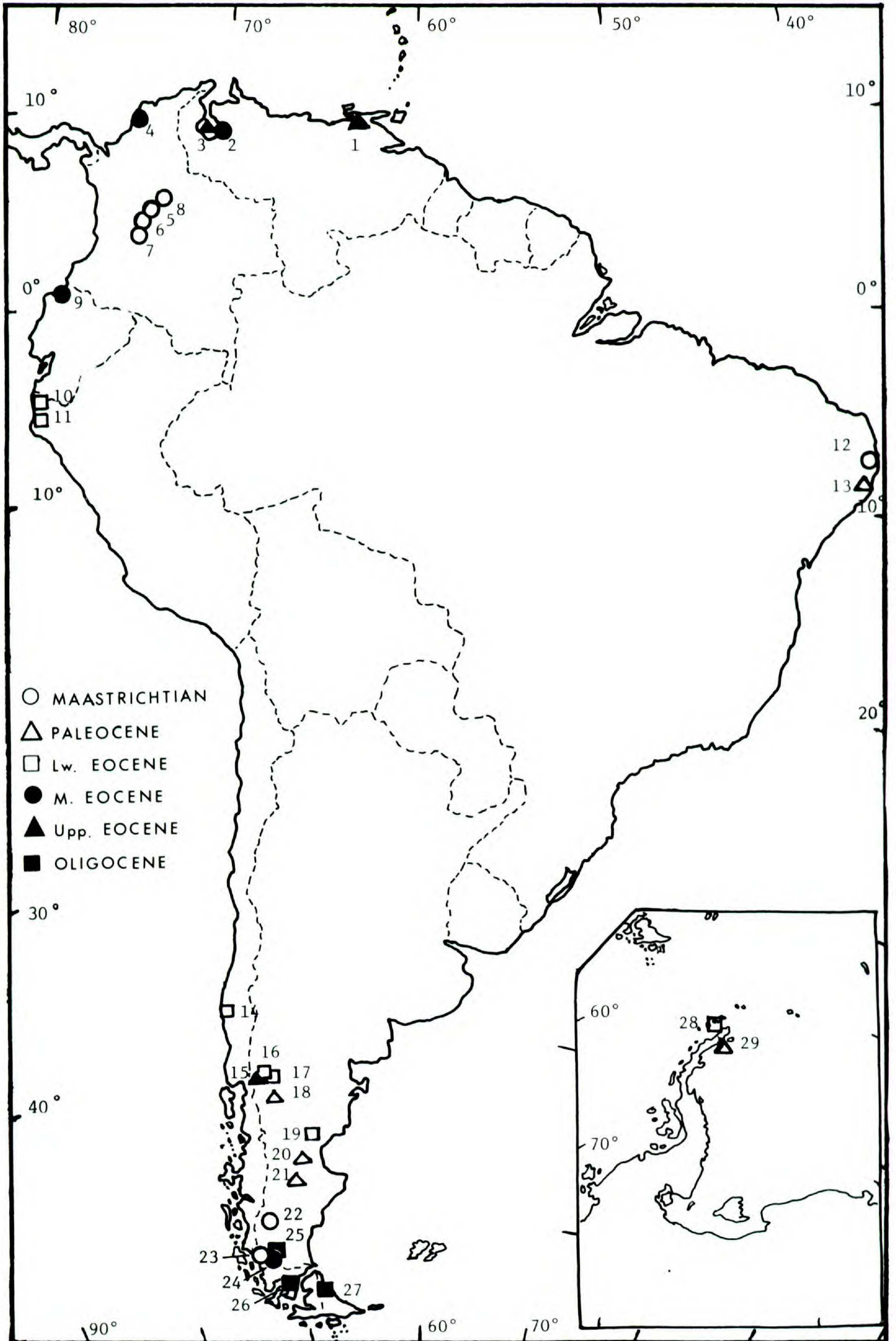
Paleoflora. A fossil flora that may be characterized by its systematic list, and so differentiated from other fossil floras. Each paleoflora may comprise several taphofloras. From the characteristic systematic list a characteristic plant association may be hypothesized, and so vegetational features suggested.

A REVIEW OF THE PALEOGENE TAPHOFLORAS OF SOUTH AMERICA

Figure 1 shows the positions of the known Paleogene taphofloras, and some Late Cretaceous and Early Neogene ones. They are located on the margins of several marine basins that existed

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² Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Guiraldes 2620, 1428 Buenos Aires, República Argentina. Member of Consejo Nacional de Investigaciones Científicas (CONICET).



during the Upper Cretaceous and Lower Tertiary (Fig. 2). These basins are related to similar ones of the Upper Cretaceous and the Oligocene-Miocene (Bertels, 1979; Zambrano, 1981), which changed considerably the configuration of the continent. Most of the fossil floras have been buried in deltas, coastal swamps, or lagoons.

MAASTRICHTIAN

Included here are the outcrops of the Gauduas Formation in the vicinity of Bogotá, Colombia, originally described as Miocene, but they correspond to the Maastrichtian according to van der Hammen (1954). These outcrops are located in Cipacón (Fig. 1.6) and Zipaquina (Fig. 1.7) (Department of Cundinamarca), El Infierno (Fig. 1.5) (Department of Boyacá), and Falls of Tequendama (Fig. 1.8) near Bogotá. Fruit casts and leaf imprints have been described: among the former, *Humiria cipaconensis* (Berry, 1924a; Selling, 1945); among the latter, *Geonomites zipaquinensis*, *Ficus andrewsi*, *Coussapoa camargoi*, *C. ampla*, *Nectandra lanceolata*, and *Theobroma fossilium* (Berry, 1929a; Huertas, 1960). *Humiria* was also found in Belén, Perú (Lower Eocene) (Berry, 1927, see below). The palynological record shows that northern South America was a province rich in American elements, where palms dominated (van der Hammen, 1954).

In Brazil, *Palmocarpon luisi* is quoted in the Paraíba Group (Fig. 1.12) in Paraíba state (Mauzy, 1936).

In southernmost South America, the taphoflora of Cerro Guido (Fig. 1.23) has approximately 30 species of leaf imprints, most of which have been attributed to Lower Cretaceous species of North America. They have been studied by Kurtz (1899), with a few additions by Hunicken (1971), and Menéndez (1966, 1972a, 1972b). Many have palmatilobate leaves.

The deposits of the Mata Amarilla Formation, though of Coniacian age (earlier than the Maas-

trichtian) (Romero, 1978), are also worth mentioning because they present some species that migrated to Australasia during the Paleogene. Among them, some have or have had a cosmopolitan distribution (*Hymenophyllum*, *Podocarpus*), but others are mainly southern (*Dacrydium*, *Gleichenia*). Some extended as far as New Zealand (*Blechnum*, *Laurelia*) during the Tertiary.

Fossil leaves of *Nothofagus* have not yet been found in the South American Maastrichtian, but a few pollen grains have been found, already differentiated into three types (*fusca*, *brassi*, and *menziesii*) in sites some 1,500 km apart (Archangelsky & Romero, 1974; Romero, 1973). The site of the plants that produced these pollen grains has not yet been discovered.

PALEOCENE

Paleocene taphofloras are not known in northern South America, but the palynological evidence (Muller, 1970, 1981) already indicates the presence of Bombacaceae (*Bombax* type). In northeast Brazil (Fig. 1.13), fruits of *Nypa pernambucensis* and *Celtis santosi* and imprints of *Psidium* have been found (Beurlen & Sommer, 1954; Dolianiti, 1955).

In southern South America the oldest Tertiary deposit is that of Funes (Fig. 1.20) of Danian age (Berry, 1937a; Romero, 1978), probably together with that of Sur del Río Deseado (Fig. 1.21) (Arguijo & Romero, 1981; Hunicken, 1968; Spaggiari, 1924). In these, 11 and three species have been discovered respectively, of which only one is found in other deposits. All the species seem to belong to subtropical genera of the Neotropical Region.

The information on these taphofloras may be complemented with the results of palynological (Archangelsky, 1973, 1976a, 1976b) and paleo-xylological studies (Petriella, 1972), which culminated with a paleoenvironmental reconstruction (Petriella & Archangelsky, 1975). This

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FIGURE 1. Paleogene taphofloras of South America.—1. Santa Bárbara, Trujillo Venezuela.—2. Escuque, Venezuela.—3. Maracaibo, Venezuela.—4. Dpto. Bolivar, Colombia.—5. El Infierno, Boyacá, Colombia.—6. Cipacón, Cundinamarca, Colombia.—7. Zipequina, Cundinamarca, Colombia.—8. Tenquendama, Colombia.—9. Ancon, Ecuador.—10. Sur de Talara, Perú.—11. Belén, Perú.—12. Paraíba, Brasil.—13. Pernambuco, Brasil.—14. Lota y Coronel, Chile.—15. Niriuhau, Argentina.—16. Río Pichileufú, Argentina.—17. Río Chenqueniye, Argentina.—18. Laguna del Hunco, Argentina.—19. Cañadón Hondo, Argentina.—20. Funes, Argentina.—21. Sur del Río Deseado, Argentina.—22. Mata Amarilla, Argentina.—23. Co Guido, Chile.—24. Río Turbio, Argentina.—25. Río Guillermo, Argentina.—26. Loreto, Chile.—27. Río Leona, Argentina.—28. La 25 de Mayo, Argentina.—29. La Seymour, Argentina.

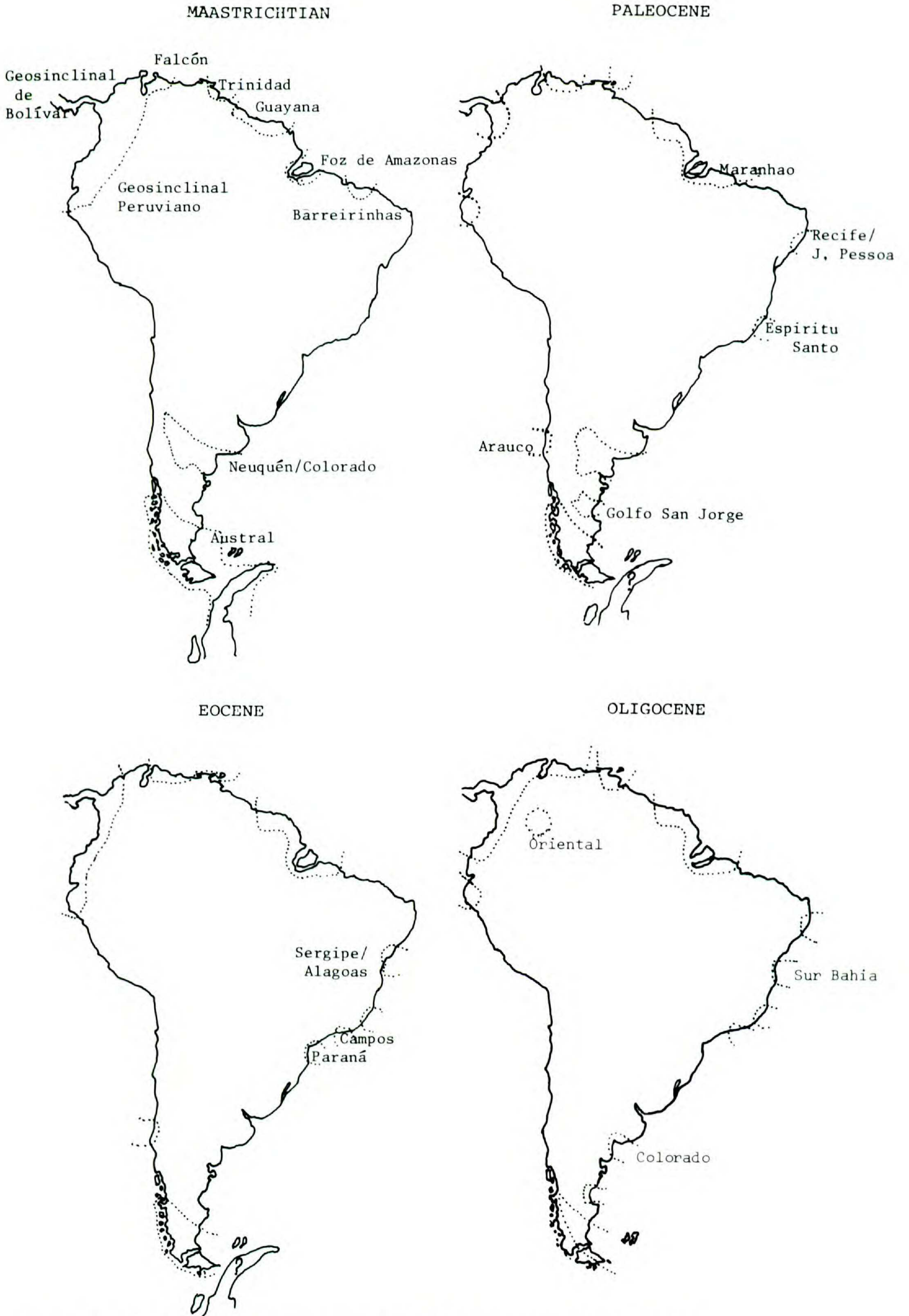


FIGURE 2. Marine basins in South America. From Bertels (1979), slightly modified.

reconstruction showed in the region of Golfo San Jorge (latitude 46°S) a vegetation section similar to the one found today in southern Brazil, some 2,000 km and 20° further north. It includes mangrove communities, swamp forest, tropical rain forest, mountain rain forest, highland forest, and sclerophyllous forest or savanna. The climate must have been subtropical humid. This coincides with the findings of crocodiles, which indicate that the 10° July isotherm passed through the region at that time, whereas at present it is some 1,500 km further north (Volkheimer, 1971).

Among the genera that constituted these communities, several were of Australasian origin such as *Dacrycarpus*, *Dicranopteris*, and *Gunnera*, and *Tricolpites fillii*, similar to *Beauprea*, which existed in New Zealand during the Cretaceous. Other elements appear simultaneously in New Zealand and South America, such as *Anacolosa* and *Nypa*, although they were not as frequent in South America as in Australasia. *Nypa* must have had a wide distribution because it has also been found in Pernambuco (Brazil) in Paleocene deposits. Other genera appear in these sediments for the first time, reaching New Zealand during the Eocene and Oligocene (*Retidiporites camacho*, having affinities with *Banksia*, *Weinmannioxylon*, etc.).

The taphoflora of Laguna del Hunco (Fig. 1.18), in northwest Patagonia, is at least 59 million years old, as established by isotope dating (Archangelsky, 1974). It has some 25 described species (Berry, 1925), to which Petersen (1946) added a list of over 70 determinations. It has 69% of entire margined leaves. This percentage corresponds to the Paratropical Rain Forest according to Wolfe (1971, table 1) and to the Tropical Seasonally Dry climatic zone according to Dilcher (1973a, fig. 4). This taphoflora includes several genera of the present Neotropical Region (*Annona*, *Cochlospermum*) and others of the present Antarctic Region (*Lomatia*, *Peumus*), although it does not contain *Nothofagus*. Furthermore, endemics to the present Australian Region (*Casuarina* and *Akania*, Frenguelli, 1943; Romero & Hickey, 1976) and subtropical genera of xeric type (*Schinopsis*) have also been found in this taphoflora.

At a latitude of some 22° and 2,000 km further south is the taphoflora of Seymour Island (Fig. 1.29) (Isla C. Marambio in Argentine maps; Dusen, 1907). Its age is probably equivalent to that of Laguna del Hunco, since it seems to belong to the Paleocene Cross Valley Formation, ac-

ording to Elliot and Trautman (1982). Dusen described 25 species and 64 forms determined to genera, especially of Pteridophyta, and he was the first author to point out the existence of a mixture of "temperate species" with "species similar to those of southern Brazil" or "subtropical" (Dusen, 1907). This taphoflora is presently found at a latitude of 64°31'S. It has 42% of entire leaves, which corresponds to a Subtropical Forest (Wolfe, 1971, table 1) or to Warm Temperate, probably moist, climatic zone (Dilcher, 1973a, fig. 4).

LOWER EOCENE

In northern South America the Lower Eocene is represented in Peru by the deposits of Sur de Talara (Fig. 1.10) and Belén (Fig. 1.11). The former was described (Berry, 1929b) as belonging to "Restin Formation" but in fact it corresponds to the Chacras Formation (Hoffstetter, 1956; Bertels, 1979). Berry described some of the fruits he studied as *Attalea olsoni*, *Iriartites restinensis*, and *Carpolithus jathrophaformis*. The second deposit (Belén) lies in the Pariñas Sandstone of Lower Eocene age (Hoffstetter, 1956). From these Berry, (1927, 1937c) described 11 species, belonging to genera such as *Palmacarpus*, *Humuria*, *Sapindoides*, *Cupanoides*, and *Anacardium*. The climate was "humid, lowland tropical," according to Berry (1927).

The deposits of Lota and Coronel (Fig. 1.14) in Chile are at a latitude of 37°S. Their age is Lower Eocene, although some authors consider it to be Paleocene (Palma Heldt, 1980). Engelhart (1891, 1905) and Berry (1922) described over 100 species, all of them assigned to Neotropical genera.

Berry expressed the opinion that "its elements are represented by modern species of tropical South America east of the Andes, and in the main of forms dwelling in the Amazon basin, especially toward the Peruvian part of the basin, and extending southward into eastern Bolivia . . . I would estimate the Chilean fossil flora as indicating a change from the present climatic conditions corresponding to from 10° to 12° of latitude at sea level." About the climate he said that "there was never frost" and it was "very much warmer and with more sunshine than at the present time." The percentage of species with entire margined leaves (70%) would indicate that it was a Paratropical Forest, in the sense of Wolfe (1971) or a Tropical, Seasonally Dry climatic zone in the sense of Dilcher (1973a).

In northwest Patagonia, the Lower Eocene is represented by two important deposits: Río Pichileufú (Fig. 1.16) and Río Chenqueniyeu (Fig. 1.17). Three species described from the outcrop of Alto Río Ñirihuau (Fiori, 1939) may be considered with the last one. All are thought to belong to the Ventana Formation (Aragón & Romero, 1984). They include some 140 species and 40 species respectively (Berry, 1938; Fiori, 1940) with a mixture of Neotropical and Antarctic elements. The first of these deposits is essentially similar to that of Laguna del Hunco, described above, and its percentage of entire-margined leaves is 69%. Berry (1938) pointed out the presence of genera that are a) tropical or subtropical, b) temperate, c) of semiarid environments (*Cupania*, *Schinopsis*, and *Schinus*), d) "from the temperate rain forest region of southern Chile," and e) 14 genera of possible lianas. The conditions were of humid and warm climate, judging from the flora, but the mixtures of elements did not allow Berry to classify them with certainty.

The taphoflora of Río Chenqueniyeu is also mixed, and very similar to the previous one, but it does include *Nothofagus*.

Somewhat further south, in the Basin of Golfo San Jorge, lie the deposits of Cañadon Hondo (Fig. 1.17), of which Berry (1932a) studied several small taphofloras. Their age is considered to be Eocene according to Andreis (1978) and they contain Neotropical and Subantarctic elements (see Romero, 1978, for a discussion of unpublished material).

Finally, some 2,000 km to the south, leaf imprints also are found (Orlando, 1963) in the taphoflora of Isla 25 de Mayo (King George) (Fig. 1.28) of the Antarctic Peninsula, at a latitude of 64°S. It contains Antarctic elements such as *Laurelia* and *Nothofagus*, but together with Neotropical ones such as *Schinopsis* and *Nectandra*. It may be especially compared with the taphoflora of Río Pichileufú. The total number of described species is only ten, but seven are entire margined. Although the number of species is not sufficient for a statistical analysis, it seems evident that the association was not less warm than subtropical. The age, given originally as Miocene, is considered to be Lower Eocene (Arguijo & Romero, 1981; Romero, 1978).

MIDDLE EOCENE

In the Department of Bolívar, Colombia (Fig. 1.4), Berry (1924b, 1929a) described several fossil fruits that he attributed to the Middle Eocene.

These are *Sapindoides peruviana*, *Carpolithus bolivariensis*, and *Celtis bolivariensis*. In Venezuela near Escuque (Fig. 1.2), Berry (1920) discovered *Entada boweni*, of the Escuque Formation (Middle Eocene, Hoffstetter, 1937). In Ecuador, the area of Ancón (Fig. 1.9), Península de Santa Elena, yielded fruits of angiosperms (Berry, 1929c, 1932b). According to the collector (Sheppard, 1937) the fossils came from the Socorro Sandstone (Middle Eocene, Hoffstetter, 1936). The material includes *Astrocarym sheppardi*, *Ventanea sheppardi*, *Palmocarpon bravoii*, *Annona peruviana*, and *Sapindoides peruvianus*. The last three are also found in the deposit of Belén, and the last is also found in the Department of Bolívar, Colombia. The genera belong to a Neotropical lineage, and the environment that they indicate is a lowland rain forest.

In Patagonia, the fossil floras of the Middle Eocene are represented in the Río Turbio Formation (Fig. 1.24). This important formation contains several levels with imprints, which were studied by Berry (1937b), Frenguelli (1940), and Hunicken (1955, 1967). The levels "s" and "t," which were studied specially by the last author, contain a mixture of Neotropical and Antarctic genera, including *Nothofagus*. The pollen analysis indicated that in several levels the pollen grains of *Nothofagus* may be dominant (Archangelsky & Romero, 1974; Romero, 1977). The percentage of entire-leaved species is 40%, which would indicate a Subtropical Rain Forest (Wolfe, 1971) or a Warm Temperature, moist, climatic zone (Dilcher, 1973a).

UPPER EOCENE

The Upper Eocene is represented in Venezuela, near Santa Bárbara (Fig. 1.1), Zulia State (Berry, 1936), and in the basin of Maracaibo (Fig. 1.3) (Berry, 1939). Berry described leaf imprints of nine species already known in, or linked to, the floras of the Coastal Plain of North America. They belong to the genera *Apocynophyllum*, *Burserites*, *Cedrela*, *Chrysophyllum*, *Ficus*, *Inga*, *Terminalia*, and *Combretum*, suggesting the extension "of an equable and warmer climate north of the equatorial zone."

In northwest Patagonia, approximately at the latitude at which paratropical rain forest developed during the Lower Eocene, several outcrops with leaf imprints were found in the Ñirihuau Formation (Fig. 1.15) (Aragón & Romero, 1984; Berry, 1928; Feruglio, 1941; Fiori, 1931, 1939; Romero & Arguijo 1981a). Altogether these out-

crops have yielded some 45 species of Antarctic genera. They are strongly dominated by genera such as *Nothofagus*, *Araucaria*, and *Lomatites*. The percentage of species with entire margin decreases to 27% representing a Mixed Mesophytic Forest according to Wolfe (1971) and Cool Temperature, moist, climate zone according to Dilcher (1973a).

OLIGOCENE

No confirmed records of Oligocene plants are known to me from northern South America. Some deposits attributed to that age are actually older, such as that of Pariñas Sandstone in Belén, Perú, or that of Falls of Tequendama, Colombia, mentioned above.

In the southern extreme of the continent there are plant imprints in several taphofloras of the Río Guillermo (Fig. 1.25), Río Leona (Fig. 1.27), and Loreto Formations (Fig. 1.26) (Dusen, 1899; Frenguelli, 1940; Gilkinet, 1912; Hunicken, 1955). The first of these lies unconformable on the Río Turbio Formation mentioned above, and its age was established as Oligocene-Miocene by Hunicken (1955). The Río Leona Formation is considered to be correlated with the lower section of the Río Guillermo Formation (Russo et al., 1980). The Loreto Formation is considered to be Upper Eocene or Oligocene (Fasola, 1969), slightly more modern than the Río Turbio Formation. Arguijo and Romero (1981) found that the fossils contained in these three formations are very similar (Jaccard index ca. 50). Consequently, it seems logical to consider the taphofloras of the three formations together, and attribute them for the moment to the earlier Oligocene, or perhaps to the later Eocene.

The leaf imprints represent 27 species of *Fagaceae* and associated plants of the Antarctic Region, although Dusen (1899) pointed out that the greatest affinities of the flora are with the associations presently limited to the northern extreme of the Subantarctic Province, some 1,000 km north of the fossiliferous outcrops. The percentage of entire margined leaves is similar to that of the Ñirihuau taphoflora, of the Upper Eocene, but the size of the leaves seems to be substantially smaller, generally nanophylls, or at the most microphylls.

MIOCENE

Outcrops of Miocene age with plants are abundant in South America and some of them are

classical, such as those of Loja and Cuenca Basins (Ecuador), but their consideration lies outside the scope of the present work.

It is noteworthy that they are absent from Patagonia and the southern part of Chile. Thus they reflect a change in the deposition regimes as was pointed out by Yrigoyen (1969), and Pascual and Odreman Rivas (1971), based on different kinds of evidence. Furthermore, many of them that indicate humid, lowland tropical forest appear in present day highlands or desert areas, thus making it possible to establish, together with others of Pliocene and Pleistocene ages, the time at which the Andes started to rise, producing changes that lead to the formation of deserts and highland environments (Menéndez, 1971; Axelrod, 1979).

DISCUSSION

PALEOPHYTOGEOGRAPHY

The living vegetation of South America belongs to two botanical Regions: Neotropical and Antarctic (Cabrera & Willink, 1973). The Neotropical Region covers most of the continent under an array of very variable climatic conditions. Wet forests comprise the Caribbean, Amazonian, and Guayanan Dominions; drier and poorer forests correspond to open areas without trees and comprise the Chaqueño and Andino-Patagonian Dominions. The Antarctic Region contains a wet to rather dry forest, in the only Subantarctic Dominion.

Figure 3 shows the taphofloras discussed in the previous section placed according to their age and approximately at their present latitudes. I used present latitudes because the plotted outcrops belong to different ages. Furthermore, the South American continent has not migrated very much since the Cretaceous. According to Valencio et al. (1971), in Cretaceous times it was about 10° more to the north, and a slow, uniform, non-rotating displacement has occurred since then.

Three main sectors may be observed in Figure 3. The first one at the upper left contains all the taphofloras with genera of the Neotropical Phytogeographic Region or their ancestors, exclusively. These taphofloras constitute the *Neotropical Paleoflora*. The second one, at the upper right, contains the taphofloras with genera characteristic of the Antarctic Phytogeographic Region, or their ancestors. This is the *Antarctic Paleoflora*. Between them, the third sector contains the floras that seem to present a mixture of species of both lineages. This is the *Mixed Paleoflora*.

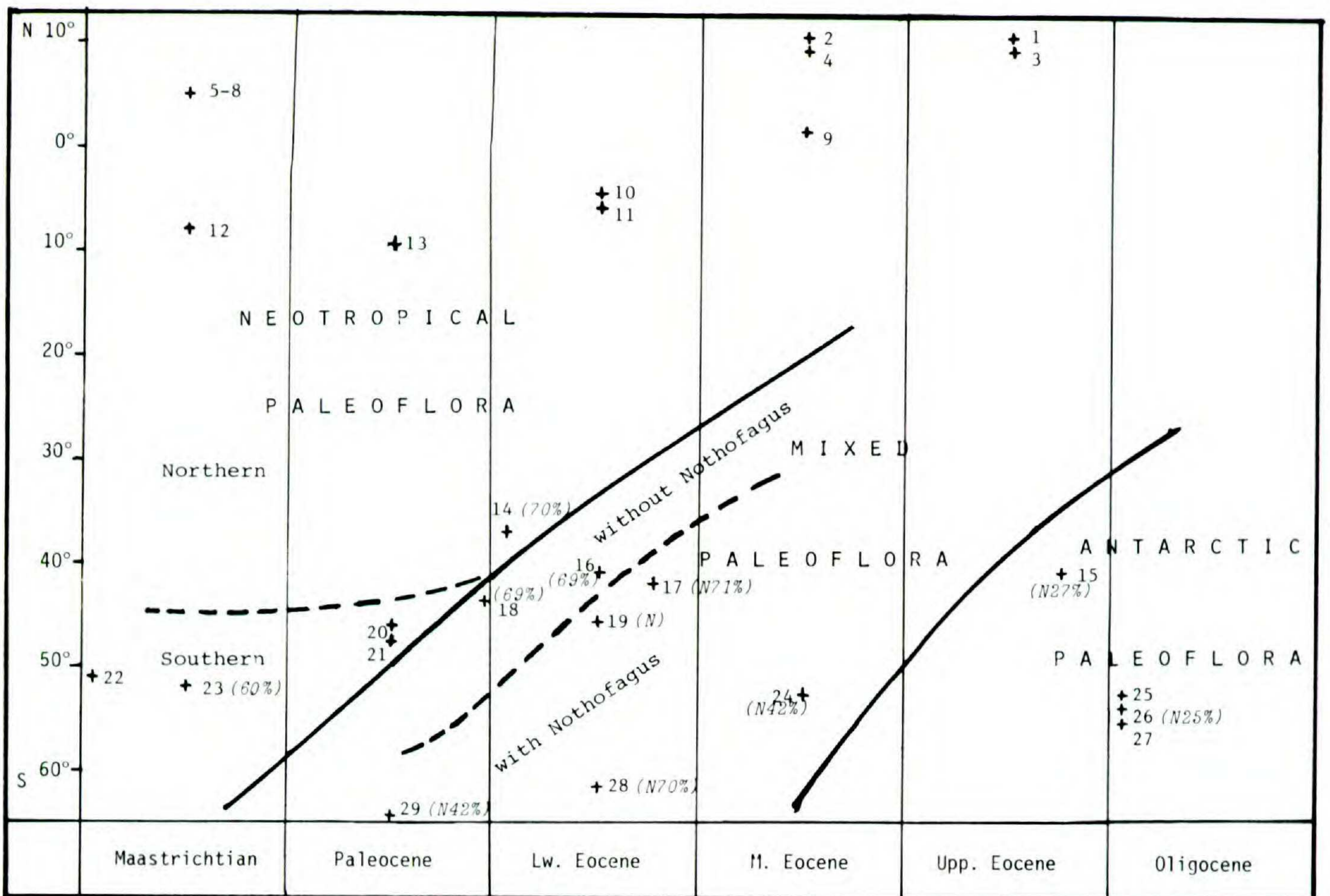


FIGURE 3. Age of Paleogene taphofloras of South America. See numbers in caption of Figure 1. Solid lines separate the paleofloras. Dashed lines separate probable provinces within them. Percentages of entire-margined leaves and the presence of *Nothofagus* (N) are denoted.

The neotropical taphofloras cover almost all South America during the entire period considered in this paper. The antarctic ones covered only the southern area from the Upper Eocene onward. The mixed ones covered almost all of Patagonia to the Antarctic between the Upper Paleocene and the Middle Eocene.

According to Dusen (1899), mixed floras were explained by an altitudinal zoning of the species, where those belonging to the Antarctic Region occupied the uplands, and those of the Neotropical Region the lowlands. I (1978) suggested that these taphofloras constituted the remainders of a stable phytogeographical unit with definite characteristics and particular ecological requirements, without strict equivalence with present plant formations, which I called *Mixed Paleoflora*.

Coincidentally, Dilcher (1973a) pointed out that in the past, both Asa Gray and R. W. Brown added genera that they considered temperate to the floras of Kentucky and Tennessee. But rather than mix these temperate forms in to so-called subtropical coastal flora, they postulated their

source area in the Appalachian uplands. At present, several authors have ceased to consider those floras subtropical, and Dilcher is of the opinion that they were "probably temperate forms present in the lowland community which we would not recognize as elements of a lowland flora today."

Also, Kemp (1978) found that, in Australian Eocene outcrops known palynologically, there is an "anomalous mixture of tropical or subtropical rainforest types with those of cool temperate rainforest communities . . . (which) . . . suggests that the early Tertiary vegetation cannot be represented by a single modern forest type. It may be that the climate regime which supported this forest has no modern analog."

I suggested earlier (Romero, 1978) that the *Mixed Paleoflora* would be characterized by a mixture of genera from other units, whose species would have had, however, ecological requirements different from the living species of the same genera, and by genera of its own, linked with the present Chaqueño Dominion. I espe-

Species	Upper		Lower Tertiary								
	Paleoflora:	Cretaceous	Antarctic		Mixed				Neo-tropical		
			26	25	16	18	24	28		19	17
<i>Schinopsis</i> sp.		*									
<i>Schinopsis</i>											
<i>patagonica</i>						*			*		
<i>balansiformis</i>					*	*					
<i>moronghifolia</i>					*						
sp. 1								*			
sp. 2								*			
cf. <i>Schinopsis</i>										*	
<i>Schinus molliformis</i>					*						
<i>Anacardites</i>											
<i>pichileufuensis</i>					*						
<i>brittoni</i>					*						
<i>patagonicus</i>										*	
sp.								*			
<i>Astronium argentinum</i>					*	*					
<i>Roophyllum</i>											
<i>serratum</i>				*				*			
<i>nordenskjoldi</i>				*					*		

FIGURE 4. Evolution of Anacardiaceae in southern South América from Cretaceous to Paleogene, from Romero (1978). See numbers in caption of Figure 1.

cially emphasized the evolution of the Anacardiaceae family in Patagonia, which, with only one species in the Coniacian (Upper Cretaceous), radiated during the Lower Tertiary, having five genera and 14 species in taphofloras of the *Mixed Paleoflora* (Fig. 4). Among those genera are *Schinopsis*, *Schinus*, and *Astronium*, which are conspicuous today in the Chaco, Caatinga, and Monte Provinces (Cabrera & Willink, 1973).

In the *Neotropical Paleoflora* a few taphofloras present elements now endemic to the Australian Region as discussed above. Upon this basis, it is possible to separate a northern, purely American Province, from a southern one, subject to migration (Fig. 3). In the *Mixed Paleoflora*, the absence of *Nothofagus* from taphofloras in Figure 3.16, 3.18, allows the separation of two provinces. Another separation is tempting, isolating taphofloras in Figures 3.24, 3.29, on the basis of their low percentage of entire-leaved species. However this is a physiognomic characteristic, and phytogeographic limits are being established in this paper on a floristic basis.

I therefore tentatively suggest that the *Neotropical Paleoflora* developed during the Lower Tertiary and was the forerunner of the more humid Dominions of the Neotropical Region (Ca-

ribbean, Amazonian, and Guayanan); that the *Mixed Paleoflora*, from the Upper Paleocene onward, gave origin to the drier Dominions (Chaqueño and Andino-Patagonian), and that the *Antarctic Paleoflora*, since the Upper Eocene, was the antecedent in South America of the Antarctic Region, represented today only by the Subantarctic Dominion. The real significance of further differences within the paleofloras is not yet apparent.

CLIMATIC CHANGES

Figure 3 shows the taphofloras discussed above and the corresponding paleofloras. The presence of *Nothofagus* was also denoted in several of them. Furthermore, the percentage of entire-leaved species was added in other cases. The merits of this last feature has been discussed by Dolph (1979), Dilcher (1973a), and Wolfe (1971, 1979) but ever since the observations of Bailey and Sinnott (1916), the high percentage has been considered a good indication of warm environment.

The areas covered by the different climatic types circumscribed on the basis of percentages of entire-margined leaves in South America do not coincide with the phytogeographical limits

of the *Neotropical*, *Mixed*, and *Antarctic Paleofloras*, as here defined. As an example, warm climates indicated by high percentages are present in both Provinces of the *Neotropical Paleoflora* and both Provinces of the *Mixed Paleoflora*. This is in accordance with the climatic variations within present Phytogeographic Regions (the Neotropical Region extends from the Amazonian wet warm forest to the Patagonian dry cold steppe) today and reflects the criteria used in this paper, whereas the Phytogeographic Regions were defined, as the recent ones are, on a taxonomic basis, and the climatic types were defined on a physiognomic basis.

The physiognomic analysis is relevant in this paper only for those taphofloras of Patagonia, because the rest, from northern South America, contain too few species for statistical analysis (Wolfe, 1975). The percentages used are mostly those given by Volkheimer (1971).

As shown in Figure 3, for the Maastrichtian, the taphoflora of Cerro Guido (Fig. 3.23) in southwest Patagonia, has 60% of species with entire-margined leaves.

For the Paleocene and early Eocene there are records in northwest Patagonia (taphofloras in Fig. 3.14, 3.16, 3.17) of 70% with entire-margined leaves. In the Antarctic peninsula there is an increase from 43% (Paleocene, Fig. 3.29) to about 70% (early Eocene, Fig. 1.28). Finally, during the late Paleocene, eastern Patagonia had a subtropical humid climate, with mangroves, crocodiles, etc., as explained above. Therefore, it may be accepted that since Maastrichtian to lower Eocene times a progressive temperature increase occurred.

For the Middle Eocene there is only a record in the Río Turbio taphoflora (Fig. 3.24), southwestern Patagonia, with a decrease up to 49% of entire-margined leaves. For the upper Eocene the Ñirihuau taphofloras (Fig. 3.15) in northwest Patagonia show a further decrease to 17%. And during the Oligocene, again in southwest Patagonia, the same percentage remains, with a dominance of small-sized leaves. Therefore, a deterioration of climate since Middle Eocene to Oligocene may be supposed.

Roughly speaking, the sequence of floras in Patagonia would imply variations from the equivalents of a Paratropical Rain Forest (Lower Eocene) to a Subtropical Forest (Middle Eocene), then to the Mixed Mesophytic Forest (Upper Eocene), and finally to a Mixed Northern Hardwood Forest (Oligocene) (*sensu* Wolfe, 1971).

In other parts of the world, a progressive temperature increase was detected during the Paleocene and Lower Eocene (Wolfe, 1978), although "cool intervals occurred during the late Paleocene, the late early to early Middle Eocene and the early Late Eocene" (Wolfe, 1978). The most important increase, during the late Eocene, is correlated with the Bertonian, although its "duration and exact timing is unknown" (Wolfe, 1975: 50). This brief shift was called the Eocene Terminal Event.

Finally, a major shift during the Oligocene was recorded in Europe, western Siberia, New Zealand, and western North America (Wolfe, 1971). It was more marked during the middle Oligocene and produced a spectacular transformation in the high latitude floras, which changed from having high percentages of large, evergreen broad leaves with entire margins to high percentages of dentate, small, deciduous leaves.

The data from South America are not abundant enough to show minute changes during the late Paleocene to the early late Eocene. However, a coincidence with the general trends to higher temperatures in other continents may be detected during the Paleocene and Lower Eocene, and then a deterioration through the Middle and Upper Eocene. The subsequent major shift during the Oligocene, however, is not yet apparent in this continent.

LITERATURE CITED

- ANDREIS, R. 1978. Geología y Sedimentología de Cañadón Hondo Pcia. de Chubut (Obra del Centenario). *Revista Mus. La Plata* 4: 77-102.
- ARAGÓN, E. & E. ROMERO. 1984. Geología, paleoambientes y paleobotánica de yacimientos Terciarios del occidente de Río Negro, Neuquén y Chubut, República Argentina. *Actas IX Congr. Geol. Argent.* 4: 475-507.
- ARCHANGELSKY, S. 1973. Palinología del Paleoceno de Chubut. I. Descripciones sistemáticas. *Ameghiniana* 10: 339-399.
- . 1974. Sobre la edad de la tafloflora de Laguna del Hunco, Provincia de Chubut. *Ameghiniana* 11: 413-417.
- . 1976a. Palinología del Paleoceno del Chubut. II. Diagramas Polínicos. *Ameghiniana* 13: 43-55.
- . 1976b. Palinología del Paleoceno del Chubut. III. Análisis numérico. I. Introducción y matrices de similitud. *Ameghiniana* 13: 169-184.
- & E. J. ROMERO. 1974. Los registros más antiguos de *Nothofagus* (Fagaceae) de Patagonia (Argentina y Chile). *Bol. Soc. Bot. México* 33: 13-30.
- ARGUIJO, M. H. & E. J. ROMERO. 1981. Análisis biostratigráfico de formaciones portadoras de tafo-

- floras terciarias. *Actas VII Congr. Geol. Argent.* 4: 691-717.
- AXELROD, D. I. 1979. Desert vegetation, its age and origin. Pp. 1-72 in J. R. Goodin & D. K. Northington (editors), *Arid Plant Resources*. International Center Arid & Semi Arid Land Studies, Lubbock, Texas.
- BAILEY, I. W. & W. E. SINNOT. 1916. The climatic distribution of certain types of Angiosperm leaves. *Amer. J. Bot.* 3: 24-39.
- BERRY, E. W. 1920. Tertiary fossil plants from Venezuela. *Proc. U.S. Natl. Mus.* 59: 553-579.
- . 1921. Tertiary formations of western South America. Pp. 845-865 in *Pan Pacific Science Conference*, Washington.
- . 1922. The flora of the Concepción-Arauco Coal Measures of Chile. *Johns Hopkins Univ. Stud. Geol.* 4: 73-142.
- . 1924a. Fossil fruits from the eastern Andes of Colombia. *Bull. Torrey Bot. Club* 51: 61-67.
- . 1924b. A fossil *Celtis* from Colombia. *Torrey Bot. Club* 51: 44-46.
- . 1925. A Miocene flora from Patagonia. *Johns Hopkins Univ. Stud. Geol.* 6: 183-252.
- . 1927. Petrified fruits and seeds from Oligocene of Perú. *Pan-Amer. Geol.* 47: 121-132.
- . 1928. Tertiary fossil plants from the Argentine Republic. *Proc. U.S. Natl. Mus.* 73: 1-27.
- . 1929a. Tertiary fossil plants from Colombia, South America. *Proc. U.S. Natl. Mus.* 75: 1-12.
- . 1929b. Eocene plants from Restin formation of Perú. *Pan-Amer. Geol.* 51: 241-244.
- . 1929c. Fossil fruits in the Ancon sandstone of Ecuador. *J. Paleontol.* 3: 298-301.
- . 1932a. Fossil plants from Chubut Territory collected by Scarrit Patagonian Expedition. *Amer. Mus. Novit.* 536: 1-10.
- . 1932b. A new palm from the upper Eocene of Ecuador. *J. Wash. Acad. Sci.* 22: 327-329.
- . 1936. Tertiary fossil plants from Venezuela. II. *Proc. U.S. Natl. Mus.* 83: 335-360.
- . 1937a. A Paleocene flora from Patagonia. *Johns Hopkins Univ. Stud. Geol.* 12: 22-50.
- . 1937b. Eocene plants from Río Turbio, in the Territory of Santa Cruz, Patagonia. *Johns Hopkins Univ. Stud. Geol.* 12: 91-98.
- . 1937c. The Pariñas sandstone of Perú. *Johns Hopkins Univ. Stud. Geol.* 12: 99-106.
- . 1938. Tertiary flora from the Río Pichileufú, Argentina. *Special Pap. Geol. Soc. Amer.* 12: 1-149.
- . 1939. Eocene Plants from a well core in Venezuela. *Johns Hopkins Univ. Stud. Geol.* 13: 157-162.
- . 1940. Mesozoic and Cenozoic plants of South America, Central America and the Antillas. *Proc. VIII Amer. Sci. Congr.* 4: 365-373.
- BERTELS, A. 1979. Paleobiogeografía de los foraminíferos del Cretácico Superior de América del Sur. *Ameghiniana* 16: 273-256.
- BEURLIN, K. & F. W. SOMMER. 1954. Restos vegetais fosseis da tectónica de Bacío Calcarea de Itaboraí, Estado do Río de Janeiro. *Bol. Div. Geol. Mineral. Minist. Agric.* 149: 16-20.
- CABRERA, A. L. & A. WILLINK. 1973. Biogeografía de América Latina. Monografía 13, Ser. Biología. Organización de Estados Americanos, Washington.
- DILCHER, D. 1973a. A paleoclimatic interpretation of the Eocene Floras of southeastern North America. In A. Graham (editor), *Vegetation and Vegetational History of Northern Latin America*. Elsevier Scientific Publ. Co., Amsterdam.
- . 1973b. A Revision of the Eocene Flora of southeastern North America. *Paleobotanist* 20: 7-18. [1971.]
- DOLIANITI, E. 1955. Frutos de Nipa no Paleoceno de Pernambuco. *Brasil. Bol. Div. Geol. Mineral. Minist. Agric.* 158: 1-36.
- DOLPH, G. E. 1979. Variation in leaf margin with respect to climate in Costa Rica. *Bull. Torrey Bot. Club* 106: 104-109.
- DUSEN, P. 1899. Über die tertiäre Flora der Magellanslan der I. *Wiss. Ergebn. Schwed. Exped. Magellansland 1895-1897*, 1: 87-108.
- . 1907. Über die tertiäre Flora des Seymour Insel. *Wiss. Ergebn. Nordsk. Schwed. Südpolar-Exped. 1901-1903*, 3: 1-27.
- ENGELHARDT, H. 1891. Über Tertiärpflanzen von Chile. *Abh. Senckenberg. Naturf. Ges.* 16: 629-692.
- . 1905. Bemerkinger zu chilenischen Tertiärpflanzen. *Abh. Naturf. Ges. Isis* 1905: 69-72.
- ELLIOT, D. H. & T. A. TRAUTMAN. 1982. Lower tertiary strata on Seymour Island, Antarctic Peninsula. Pp. 287-297 in C. Creddock (editor), *Antarctic Geoscience*. Univ. Wisconsin Press, Madison.
- FASOLA, A. 1969. Estudio palinológico de la Fm Loreto (Terciario medio), provincia de Magallanes, Chile. *Ameghiniana* 6: 3-19.
- FERUGLIO, E. 1941. Nota preliminar sobre la hoja geológica "San Carlos de Bariloche" (Patagonia). *Bol. Inform. Petrol.* 18: 27-64.
- FIORI, A. 1931. Fillite terziare della Patagonia. I. Fillite della riva meridionale del Lago Nahuel Huapi. *Giorn. Geol.* 4: 101-116.
- . 1939. Fillite terziare della Patagonia. II. Fillite del Río Ñirihuau. *Giorn. Geol.* 13: 1-27.
- . 1940. Fillite terziare della Patagonia. III. Fillite del Río Cheuqueñiyen. *Giorn. Geol.* 14: 94-143.
- FRENGUELLI, J. 1940. Nuevos elementos florísticos del Magallaniano de Patagonia Austral. *Notas Mus. La Plata, Secc. Paleontol.* 6: 173-202.
- . 1943. Restos de Casuarina en el Mioceno en El Mirador, Patagonia Central. *Revista Mus. La Plata, Secc. Paleontol.* 8: 349-354.
- GILKINET, A. 1912. Quelques plantes fossiles des Terres Magallaniques. *Exped. Antarc. Belge, Result. Voyage S.Y. Belgica, 1897-1898*, Rapp. Sci. 5: 1-6.
- HOFFSTETTER, R. 1936. *Lexique Stratigraphique International, Volumen V, Amerique Latine. Fasc. 5a, Ecuador*. CNRS, Paris.
- . 1937. *Lexique Stratigraphique International, Volumen V, Amerique Latine. Fasc. 5c, Venezuela*. CNRS, Paris.
- . 1956. *Lexique Stratigraphique International, Volumen V, Amerique Latine. Fasc. 5b, Perú*. CNRS, Paris.
- HUERTAS, G. 1960. De la flora fosil de la Sabana.

- Bol. Geol. Fac. Petrol., Univ. Industr. Santander 5: 53-57.
- HUNICKEN, M. 1955. Depósitos neocretácicos y Terciarios del Extremo S.S.W. de Santa Cruz (Cuenca Carbonífera de Río Turbio). *Revista Inst. Nat. Invest. Ci. Nat., Ci. Geol.* 4: 1-164.
- . 1967. Flora Terciaria de los Estratos de Río Turbio, Santa Cruz (Niveles plantíferos del arroyo Santa Flavia). *Revista Fac. Ci. Exact., Fis. Nat. Univ. Córdoba, Secc. Ci. Nat.* 27: 139-227.
- . 1968. Sobre los tipos de *Carolites patagonica* y *Ameghinoites desiderata* Speg. *Ameghiniana* 5: 447-456.
- . 1971. Paleophytología Kurtziana III-4. Atlas de la flora fósil de Cerro Guido (Cretácico Superior), Ultima Esperanza, Chile (especímenes examinados por F. Kurtz). *Ameghiniana* 8: 231-250.
- KEMP, E. M. 1978. Tertiary climatic evolution and vegetational history in the Southeast Indian Ocean Region. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 24: 169-208.
- KURTZ, F. 1899. Contribuciones a la Paleophytología Argentina II. Sobre la existencia de una Dakotaflora en la Patagonia Austro-occidental (Cerro Guido, Gobernación de Santa Cruz) *Revista Mus. La Plata, Secc. Paleontol.* 10: 43-60.
- MAURY, C. J. 1936. O Cretaceo de Sergipe. *Monogr. Div. Geol. Mineral. Minist. Agric., Brasil* 11: 44-47.
- MENÉNDEZ, C. A. 1964. Paleobotanical evidences in regard to the origin of the flora of Argentina. *Interim. Res. Rep. Geol. Lab. Univ. Arizona* 5: 1-23.
- . 1966. La presencia de *Thyrsopteris* en el Cretácico Superior de Cerro Guido, Chile. *Ameghiniana* 4: 299-301.
- . 1969. Die fossilen Floren Sudamerikas. In *Biogeographie und Ökologie in Sudamerika. Monogr. Biol.* 2: 161-200.
- . 1971. Floras Terciarias de la Argentina. *Ameghiniana* 8: 357-371.
- . 1972a. Paleophytología Kurtziana III-8. La flora del Cretácico Superior de Cerro Guido, Chile (1-2). *Ameghiniana* 9: 209-212.
- . 1972b. Paleophytología Kurtziana III-9. La flora del Cretácico Superior de Cerro Guido, Chile (3-7). *Ameghiniana* 9: 289-297.
- MULLER, J. 1970. Palynological evidence on early differentiation of angiosperms. *Biol. Rev. Biol. Proc. Cambridge Philos. Soc.* 45: 417-450.
- . 1981. Fossil pollen records of extant angiosperms. *Bot. Rev. (Lancaster)* 47: 1-142.
- ORLANDO, H. A. 1963. La flora fósil en las inmediaciones de la Península Ardley, Isla 25 de Mayo, Islas Shetland del Sur. Contribución 79. Instituto Antártico Argentino, Buenos Aires.
- PALMA HELDT, S. 1980. Contribución al conocimiento palinológico de los mantos carbónicos del Terciario de Arauco-Concepción, Chile. *Actas II Congr. Argent. Paleontol. Bioestratigr., I Congr. Latinoamer. Paleont., II*: 175-192.
- PASCUAL, R. & O. E. ODREMAN RIVAS. 1971. Evolución de las comunidades de los vertebrados del Terciario argentino. Los aspectos paleozoogeográficos y paleoclimáticos relacionados. *Ameghiniana* 8: 372-412.
- PETERSEN, C. A. 1946. Estudios geológicos de la región del Río Chubut medio. *Dir. Gen. Min. Geol. Bol.* 59: 1-137.
- PETRIELLA, B. T. P. 1972. Estudio de maderas petrificadas del Terciario inferior del área Central de Chubut, (Co Bororó). *Revista Mus. La Plata, Secc. Paleontol. n.s.* 6: 159-254.
- & S. ARCHANGELSKY. 1975. Vegetación y ambientes en el Paleoceno de Chubut. *Actas I Congr. Argent. Paleontol. Bioestratigr.* 2: 257-270.
- RAVEN, P. & D. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539-673.
- ROMERO, E. J. 1973. Polen fósil de *Nothofagus* (*Nothofagidites*) del Cretácico y Paleoceno de Patagonia. *Revista Mus. La Plata, Secc. Paleontol. n.s.* 7: 291-303.
- . 1977. Polen de Gimnospermas y Fagaceas de la Formación Río Turbio (Eoceno) Santa Cruz, Argentina. *Fecic Editorial, Buenos Aires.*
- . 1978. Paleoecología y Paleofitogeografía de las taofloras del Cenofítico de Argentina y áreas vecinas. *Ameghiniana* 15: 209-227.
- & M. H. ARGUIJO. 1981a. Adición de la taoflora del Yacimiento "Bariloche" (Eoceno) Pcia. de Río Negro, República Argentina. *Anais II Congr. Latinoamer. Paleontol.* 2: 489-495.
- & ———. 1981b. Nota sobre algunos problemas nomenclatoriales de plantas fósiles del cenofítico de Austrosudamérica. *Bol. Asoc. Latinoamer. Paleobot. Palinol.* 8: 21-33.
- & ———. 1982. Análisis bioestratigráfico de las taofloras del Cretácico Superior de Austrosudamérica. In *Comité Sudamericano del Jurásico y Cretácico* (editors), *Cuencas Sedimentarias del Jurásico y Cretácico de América del Sur* 2: 393-406.
- & M. C. DIBBERN. 1984. Floras Cenozoicas. Pp. 373-382. In V. Ramos (editor), *Geología y Recursos Naturales de la Provincia de Río Negro. Buenos Aires.*
- & J. HICKEY. 1976. A fossil leaf of Akaniaceae from Paleocene beds in Argentina. *Bull. Torrey Bot. Club* 103: 126-131.
- RUSSO, A., M. A. FLORES & H. DI BENEDETTO. 1980. Patagonia Austral Extraandina. *Geología Regional Argentina. Acad. Nac. Ci. Córdoba II*: 1431-1463.
- SELLING, O. H. 1945. Fossil remains of the genus *Humiria*. *Svenska Bot. Tidskr.* 39: 257-269.
- SHEPPARD, G. 1937. *The Geology of South Western Ecuador.* Muby, London.
- SPEGAZZINI, C. 1924. Sobre algunas impresiones vegetales Eocénicas de Patagonia. *Comun. Mus. Nac. Hist. Nat. Bernardino Rivadavia* 2: 95-197.
- VALENCIO, D. A., B. J. J. EMPLTON & J. F. A. VILAS. 1971. Reconstrucción y evolución del Continente Gondwana. Sobre la base de datos paleomagnéticos de la propagación de los fondos de los Océanos. *Revista Asoc. Geol. Argent.* 26: 5-23.
- VAN DER HAMMEN, T. 1954. El desarrollo de la flora colombiana en los períodos geológicos. F: Maestrichtiano hasta Terciario más inferior. (Una in-

- vestigación palinológica de la formación de Guaduas y equivalentes). *Bol. Geol. Inst. Geol. Nac. Colombia*. 2: 49–106. Bogotá.
- VOLKHEIMER, W. 1971. Aspectos paleoclimáticos del Terciario Argentino. *Revista Mus. Argent. Ci. Nat. Bernardino Rivadavia, Secc. Paleontol.* 1: 241–264.
- WOLFE, J. A. 1971. Tertiary climatic fluctuations and methods of analysis of Tertiary Floras. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 9: 27–57.
- . 1975. Some aspects of plant geography of the northern hemisphere during the late Cretaceous and Tertiary. *Ann. Missouri Bot. Gard.* 62: 264–279.
- . 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *Amer. Sci.* 66: 694–703.
- . 1979. Temperature parameters of humid to mesic forest of eastern Asia and relation to forest of other regions of the Northern Hemisphere and Australasia. *Profess. Pap. U.S. Geol. Surv.* 1106: 1–37.
- YRIGOYEN, M. R. 1969. Problemas estratigráficos del Terciario de Argentina. *Ameghiniana* 6: 315–329.
- ZAMBRANO, J. J. 1981. Distribución y evolución de las cuencas sedimentarias en el continente Sudamericano durante el Jurásico y el Cretácico. *In* Comité Sudamericano del Jurásico y Cretácico (editors), *Cuencas Sedimentarias del Jurásico y Cretácico de América del Sur*. 1: 9–44.